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*THE CONSTANCY OF DESOXYRIBOSE NUCLEIC ACID IN PLANT NUCLEI**

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For a number of years considerable interest has been centered in the role of nucleic acids in cellular processes. Recently desoxyribose nucleic acid (DNA) has been shown to possess interesting characteristics that have led several workers to consider it an essential component of the gene.[1–3] DNA is probably a universal constituent of plant and animal nuclei. Its low turnover rate to radioactive phosphorus and nitrogen, in non-dividing tissues, is evidence for a chemical stability considerably greater than that of other cell components.[4, 5] Moreover, recent analytic data on the actual amounts of DNA within nuclei have suggested that it possesses a quantitative stability as well.

Computations on the amount of DNA per nucleus have been made in two ways. Chemical analyses of large numbers of cells, with the number present estimated by sample counts, have given the average amount of

DNA, per nucleus, for many thousand cells. Light absorption measurements made through a microscope have, on the other hand, yielded data on individual nuclei. Both methods involve technical difficulties and are open to certain criticisms. Nevertheless both biochemical[1, 2, 6] and microscopic[3, 7, 8] measurements by a number of different investigators have supported the concept first proposed by Boivin, Vendrely and Vendrely[1] that within the tissues of an organism the actual amount of DNA per nucleus is apparently constant.

Boivin, *et al.*, have considered that all somatic cells of an animal possess the same amount of DNA, with the gametes containing half this value. A number of discrepancies from this simple relation have been reported. Although some of these may be attributable to errors in the analytical techniques employed, at least two processes obviously involve naturally occurring variations. Ris and Mirsky[7] first showed that DNA classes with the ratio 1:2:4 occur in the rat liver associated with polyploid nuclei. It was later found[3] that such DNA classes, apparently associated with polyploidy and polyteny, occur in a variety of animal tissues. Variation of another type occurs in association with the mitotic cycle. Since DNA in several animal tissues has been found to increase in interphase preceding cell division to twice the diploid amount, interphase nuclei of dividing tissues may contain anywhere from two to four times the amount found in the haploid sperm.[3] These variations in the amounts of DNA, associated with mitosis or DNA classes, cannot be considered in disagreement with the basic tenets of Boivin's theory. It is clear that, at least in many different animal tissues, the amount of DNA per nucleus is under rather definite quantitative restrictions. Interphase nuclei of non-dividing tissues, with a few possible exceptions, have been found to contain an amount of DNA approximately 2, 4, 8, etc., times that found in the gametes. A haploid amount of DNA has been found in sperm,[1, 2] spermatids[3, 9, 10] and male and female pronuclei.[8] In general these estimates of the nucleic acids in cells are at present accurate to 10 or 20%. The question of how precisely the quantitative relations are obeyed must await more accurate techniques.

The quantitative behavior of DNA in plant tissues has as yet received little attention. Schrader and Leuchtenberger[11] have recently shown that the amount of DNA varies from tissue to tissue in Tradescantia. The data presented, although they clearly show that the amount of DNA is different in different tissues, are not extensive enough to demonstrate the type of variability. Does DNA tend to occur in the well-marked constant units found for a number of animal tissues, or, as might be inferred from the work of Schrader and Leuchtenberger, does it fail to follow any definite quantitative pattern? The present work was primarily designed to answer this question.

Material and Methods.—Two plant species have been studied in detail and two others briefly. Plants of *Tradescantia paludosa* were kindly provided by Dr. J. M. Beal of the University of Chicago. Corn plants (*Zea mays*) were obtained from several sources, particularly commercial Golden Bantam, and three strains from the collection of Dr. M. M. Rhoades of the University of Illinois. Plants of *T. canaliculata* were collected in the Chicago region, and cultivated plants of *T. "virginiana,"* differing slightly from the typical native form, came from a Chicago garden. All material was fixed in neutral 50% formalin (one part of the stock 40% formaldehyde solution to one part of distilled water, with calcium carbonate added) immediately after removal from the plant. Pieces were small, with the smallest dimension rarely exceeding 1 mm., and buds were opened to permit rapid pentration. Fixation was for at least three hours. Material was thoroughly washed, sectioned in paraffin, and stained with the Feulgen reagent for one hour after an hydrolysis in normal hydrochloric acid of 14 minutes at 60°C. In the present study, wherever possible, all tissues to be compared were mounted together on the same slide, and where this was not done, a section of tissue previously studied was mounted beside the unknown. Control sections in five of the eight slide series studied gave essentially similar values. In the remaining three the Feulgen intensity of the control sections were slightly below that usually obtained, and all values from these series were consequently raised.

The amount of Feulgen dye in individual nuclei was estimated by photometric determinations made through a microscope. The technique was approximately as described previously[3, 12] with the following exceptions: Essentially monochromatic light was isolated by a Beckman spectrophotometer with a slit width of 0.1 or 0.03 mm. Measurements were made with a Leitz achromatic-aplanatic condenser, N.A. 1.4, a 90 × Leitz 2-mm. oil immersion apochromatic objective, N.A. 1.32, and a 20 × Bausch and Lomb coated hyperplane ocular, containing an iris diaphragm to minimize distortion from internal reflection. The microscope image, enlarged 1000 times, was projected on a field diaphragm, which allowed an area 2, 3, 4 or 5 mm. in diameter, taken in the center of the nuclear image to fall on the phototube. Measurements were made with a battery-powered 1P21 electron multiplier phototube, with output leads connected to a Farrand type B control unit and a Rubicon galvanometer. Measurements of corn tissues were made at the absorption peak of the Feulgen dye, 560 mμ. Tradescantia nuclei at this wave-length were too dark to measure accurately, and consequently were measured considerably off the maximum absorption, at 615 mμ. The extinction at this wave-length was about 22% of that at 560 mμ.

Photometric determinations of biological material are subject to a variety of technical variables.[3] The most important of these in the present work were probably caused by the irregular distribution of the stainable com-

ponents in the nucleus and inaccuracies in estimating nuclear volume. A strong formalin fixative, where rapid penetration is aided by using small pieces of tissue, tends to keep the chromatin in its natural extended state. Where the nuclei measured were markedly irregular, e.g., in meiotic diakinesis, measured values tended to be low. The apparatus was calibrated

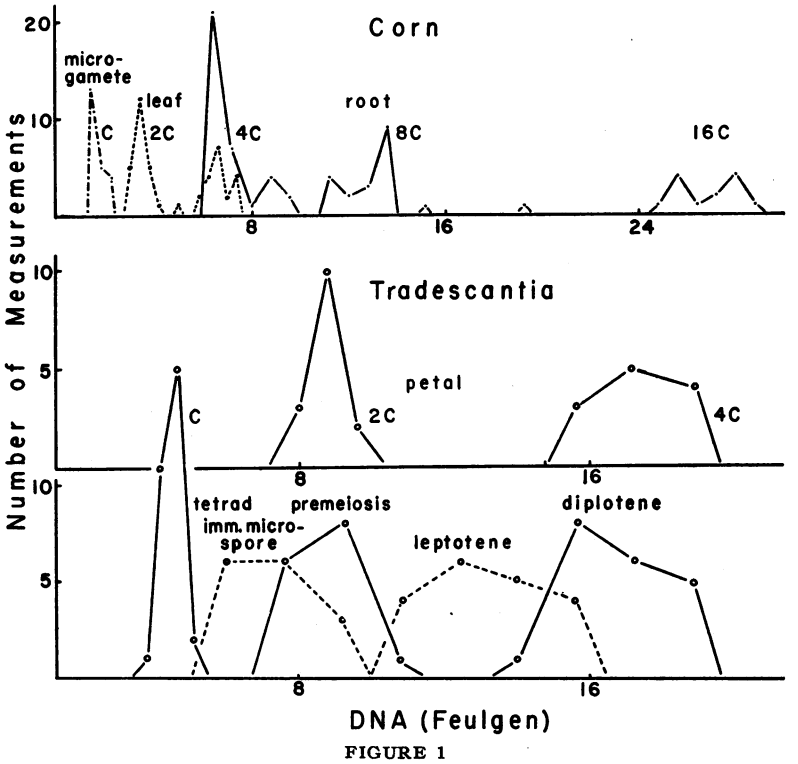

FIGURE 1

Distribution of DNA (Feulgen) measurements on individual nuclei of corn and Tradescantia tissues. The amount of DNA is shown in arbitrary units. *Upper graph:* Corn microgamete nuclei from pollen grains (dashed lines), leaf nuclei (dotted lines) and nuclei from corn root zone of elongation (solid lines). *Middle graph:* Tradescantia petal nuclei from mature flower. *Lower graph:* Stages in Tradescantia pollen formation from developing anthers, showing measurements on premeiosis (preleptotene), leptotene, diplotene, tetrad and immature microspore stages.

as previously, and the non-specific light loss was found to be negligible by measuring unhydrolyzed controls.

The advisability of using the Feulgen reaction for quantitative microphotometric determinations of DNA has been discussed by a number of workers. It is now generally agreed that, where staining procedures are properly carried out, the Feulgen reaction can give an accurate relative

estimate of the DNA in nuclei.[3, 7, 10] Since the actual intensity of the dye produced can be markedly altered by such factors as the type of fixative used, size of the tissue fixed and slight changes in hydrolysis conditions no attempt has been made here to convert the data presented into absolute amounts of DNA. All values are given in the arbitrary units used elsewhere.[3, 8] The measured extinction (E) of a central region 2 to 5 microns in diameter of an uncut nucleus has been multiplied by the squared radius of the measured area (C^2) and divided by the fraction (F) of the total nuclear volume included in the measured region. Units $= \frac{EC^2}{F}$, where $F = \frac{R^3 - (R^2 - C^2)^{3/2}}{R^3}$, and R is the radius of the nucleus. Markedly aspherical nuclei were not measured. Where nuclei were slightly ellipsoid, R was taken as the mean of major and minor axes.

Results.—(*A*) *Non-Dividing Tissues:* Photometric measurements made on tissues where mitoses were uncommon tended to fall in certain well-marked classes. Means of these classes fit in the series 1:2:4:8:16:32. The distributions of measured values from corn leaf and root, and Tradescantia petal are shown in figure 1. Means for all measurements are given in tables 1 and 2. The values are expressed as the total number of dye molecules per nucleus, in arbitrary units, and thus constitute a relative estimate of the DNA in nuclei. In similar tissues the arbitrary units are about 2.5 times higher for Tradescantia than for corn. Since the Tradescantia tissues were measured at a wave-length giving only about 22% of maximum extinction, these nuclei contain approximately 10 times the DNA found in corn.

The lowest values for Tradescantia have been found in the young microspore nuclei (tetrad stage), young generative nuclei and tube nuclei; and for corn in the microgamete nuclei of mature pollen, all presumably haploid. Most nuclei in both species were found to have twice ($2C$) or four times ($4C$) the haploid amount. Nuclei falling in class $8C$ have been found in Tradescantia stamen hairs, corn root and root cap and in the scutellum nuclei of the corn kernel. In the root and scutellum $16C$ nuclei also occur. In a few tissues, i.e., the root cap and zone of elongation in corn, and in the mature stamen hairs in Tradescantia, class $2C$ nuclei are rare and almost all nuclei belong to the higher classes. In young stamen hairs, however, class $2C$ cells are common. Measurements on the aleurone and endosperm of the corn kernel, tissues long known to be triploid through the joining of one microgamete with the $2N$ endosperm nucleus, fell in the series 3:6:12:24. Most aleurone nuclei in the kernels studied fell in class $6C$. Endosperm nuclei were measured in young ears, since those of the mature kernel are highly irregular. The smaller classes tended to be peripheral.

In the corn root zone of elongation most nuclei fell in classes 4*C* and 8*C*. However, in certain rows of cells forming the major vessels of the root, larger classes (up to 32*C*) were found. When all the nuclei in such a vessel were measured in order from the root tip back to about 1500 μ from the tip,

TABLE 1

AVERAGE AMOUNTS OF DNA (FEULGEN) PER NUCLEUS IN VARIOUS TISSUES OF CORN (*Zea mays*)

CELL TYPE	DNA CLASS	DNA IN ARBITRARY UNITS	STANDARD ERROR	NO. MEASURED
Microgamete nucleus (interphase)	*C*	1.6[a]	0.06	22
Leaf				
(interphase)	2*C*	3.4[a]	0.05	23
	2*C* → 4*C*	4.8[a]	..	1
	4*C*	6.6[a]	0.12	19
(prophase)	4*C*	6.9	0.12	10
(telophase)	2*C*	3.2	0.09	12
Root cap (interphase)	4*C*	6.9	0.12	15
	8*C*	12.6	0.33	22
Root elongation zone (interphase)	4*C*	6.6[a]	0.06	29
	4*C* → 8*C*	8.7[a]	..	6
	8*C*	12.5[a]	0.27	19
	8*C* → 16*C*	20.2[a]	..	2
	16*C*	26.1[a]	0.45	17
	16*C* → 32*C*	33.8	..	2
	32*C*	49.0	..	6
Root meristem				
(interphase)	2*C* → 4*C*	5.4[a]	0.21	36
(prophase)	4*C*	6.4[a]	0.09	15
(telophase)	2*C*	3.2[a]	0.05	20
Embryo (interphase)	2*C*	3.6	0.07	15
	4*C*	7.1	0.13	15
Scutellum (interphase)	2*C*	3.3	0.09	20
	4*C*	6.4	0.11	40
	8*C*	12.6	0.24	15
	16*C*	26.2	..	5
Aleurone (interphase)	3*C*	4.8	0.07	15
	6*C*	10.1	0.20	40
	12*C*	20.5	0.60	15
Endosperm (interphase)	3*C*	5.0	0.06	15
	6*C*	9.3	0.14	17
	12*C*	19.1	0.60	16
	24*C*	38.0	1.20	10

[a] Data graphed in figure 1 or figure 2.

all classes from 4*C* to 16 or 32*C* were usually represented, in ascending order. From 6 to 12 nuclei have been found together from each class, and between these groups anywhere from 0 to 6 intermediate values have been obtained. It is thus likely that these large vessel cells, while remaining in interphase undergo a periodic DNA doubling. Values from a few such series are com-

bined in figure 1 and table 1; in table 1 only values falling outside the expected interclass variability have been considered as intermediate. More work on this process is in progress.

Only one intermediate value has been obtained from leaf tissue in more than 150 measurements, and this came from the leaf base where a few mitoses were present. In the differentiated leaf, where cell division is absent, no intermediates have been found. It seems probable that intermediate amounts occur only when cells are synthesizing DNA for cell division (see below) or periodic DNA doubling.

(*B*) *Dividing Tissues:* The quantitative changes in DNA during the mitotic cycle were studied in corn root and leaf meristem, and in the root

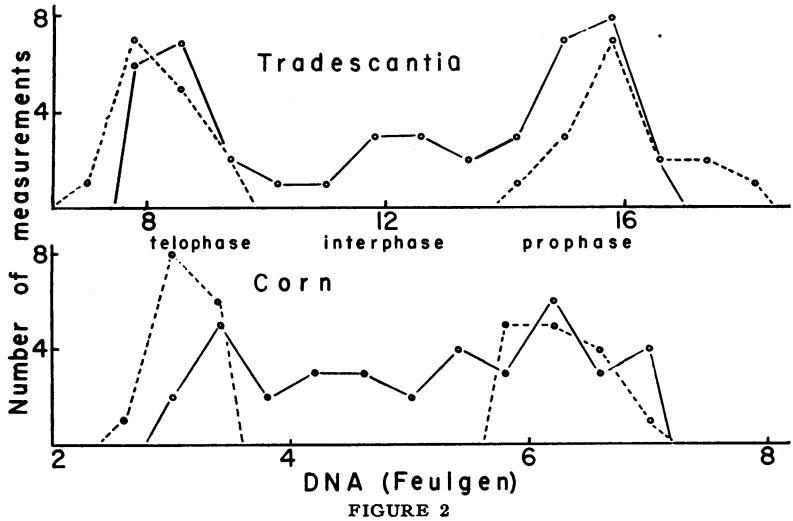

FIGURE 2

Distribution of DNA (Feulgen) measurements on individual nuclei from the root meristem of corn and Tradescantia. The amount of DNA is shown in arbitrary units. Interphase nuclei (solid lines), prophase nuclei (dotted lines at right), and telophase nuclei (dotted lines at left).

meristem and sporogenous tissue of Tradescantia. In all these tissues the process was essentially the same, paralleling that described previously for animals.[3] Where mitotic figures were common, measurements on interphase nuclei scattered widely between classes 2*C* and 4*C* (Fig. 2). Prophase values fell in 4*C* and telophases in 2*C*. Late prophase, metaphase and anaphase cells were too irregular to measure, but the behavior of DNA in these stages can easily be inferred. Apparently DNA increases during interphase to double the common diploid amount, reaching the 4*C* value at or before the visible beginning of prophase. During prophase and metaphase probably no DNA is synthesized. The 4*C* amount is then cut in

two at anaphase, and the telophase nuclei each possess the $2C$ value. In the tissues studied no $8C$ or $16C$ prophase stages have been found, although

TABLE 2

AVERAGE AMOUNTS OF DNA (FEULGEN) PER NUCLEUS IN VARIOUS TISSUES OF *Tradescantia paludosa*

CELL TYPE	DNA CLASS	DNA IN ARBITRARY UNITS	STANDARD ERROR	NO. MEASURED
Leaf (interphase)	$2C$	8.5	0.07	20
Root meristem				
(interphase)	$2C \rightarrow 4C$	13.1[a]	0.47	30
(prophase)	$4C$	16.2[a]	0.29	15
(telophase)	$2C$	8.3[a]	0.16	15
Tapetum (interphase)	$2C$	8.5	0.10	33
	$4C$	16.4	0.36	14
Petal (interphase)	$2C$	8.6[a]	0.13	15
	$4C$	16.9[a]	0.27	15
Stamen hairs (interphase)	$2C$	8.5	0.26	10
	$4C$	16.6	0.26	21
	$8C$	33.6	0.65	15
Sporogenous tissue				
(interphase)	$2C \rightarrow 4C$	13.1	1.00	15
(prophase)	$4C$	16.0	0.24	15
(telophase)	$2C$	8.1	0.19	15
Microspore mother cells				
(preleptotene)	$2C$	8.7[a]	0.20	15
(leptotene)	$2C \rightarrow 4C$	12.6[a]	0.39	15
(leptotene)	$2C \rightarrow 4C$	13.0	0.54	20
(zygotene)	$4C$	16.1	0.20	20
(pachytene)	$4C$	16.8	0.39	15
(diplotene)	$4C$	16.9[a]	0.28	20
(diakinesis)	$4C$	16.3	0.25	20
Microspores				
(tetrad stage)	C	4.4[a]	0.04	30
(early interphase)	C	4.0	0.10	20
(late interphase)	$C \rightarrow 2C$	5.9	0.34	10
(late interphase)	$C \rightarrow 2C$	7.4[a]	0.24	25
(prophase)	$2C$	9.2	0.20	15
Pollen tube nuclei				
(early interphase)	C	4.2	0.09	15
(late interphase)	C	4.1	0.07	27
Generative nuclei				
(early interphase)	C	4.3	0.11	14
(late interphase)	$2C$	8.5	0.08	16

[a] Data graphed in figure 1 or figure 2.

their occurrence might be expected in connection with the division of $4C$ or $8C$ nuclei. In the corn root zone of elongation where most interphase nuclei fall in class $4C$, cells apparently proceed directly into a $4C$ prophase without DNA synthesis, the $4C$ level then being restored in the following

interphase. In the stamen hairs of Tradescantia most cell division was found to take place in developing buds, where $2C$ nuclei were common, following the usual pattern. No division stages were seen in the $4C$ or $8C$ nuclei from mature flowers.

(*C*) *Meiosis:* The behavior of DNA during pollen formation was studied only in Tradescantia, since the chromosomal material during most meiotic stages of corn was found too irregular for measurement. Anthers of Tradescantia, when first differentiated, are filled with rapidly dividing sporogenous cells. Measurements of these cells, in young anthers, tended to follow the pattern found in other dividing tissues (table 2). Prophases fell in $4C$, telophases in $2C$, and interphases were scattered in between. The beginning of meiosis is marked by general cessation of mitotic activity in the anther, except at the periphery. The nuclei measured in this preleptotene resting stage, before the thread-like chromosome structure becomes apparent, fell in class $2C$. During the subsequent leptotene, microspore mother cells were found to increase in amount of DNA so that measurements on this stage were intermediate between $2C$ and $4C$ (Fig. 1). The next stage measured was late zygotene, where only a few unpaired strands were visible. In these cells the DNA had approximately doubled ($4C$), and throughout the rest of the meiotic prophase no further increase was found. Immediately after the second maturation division, while still in the tetrad stage, the microspore nuclei fell in class C. Measurements on microspores from three later stages of development indicate that a comparatively long period ensues during which the microspore contains the class C amount, followed by a fairly rapid increase prior to mitosis. Data for microspores from one anther, intermediate between C and $2C$, are graphed in figure 1. At early prophase of the microspore division nuclei fall in class $2C$ and are divided into tube and generative nuclei, each with the class C amount. Some time before anthesis the generative nucleus increases to $2C$, but the tube nucleus remains at the C amount. In the mature pollen most generative nuclei become very elongate and are thus impossible to measure, but a few continue to be spheroidal, and in these the DNA can be determined. The two microgamete nuclei resulting from division of the generative nucleus were not measured in Tradescantia, but the microgamete nuclei were studied in corn and fell in class C (Fig. 1 and table 1).

The course of DNA in Tradescantia meiosis can thus be outlined briefly as follows: The earliest microspore mother cells fall in class $2C$, increasing during leptotene and possibly also during zygotene to $4C$ for the remaining stages of the meiotic prophase. The four tetrad nuclei resulting from the maturation divisions each have the C amount, increasing to $2C$ before the microspore mitosis. This division results in class C tube and generative nuclei, the latter increasing to $2C$ before anthesis. The generative nucleus apparently divides to form two haploid (C) microgamete nuclei.

(*D*) *Strain and Species Differences:* As mentioned above, nuclei of *Tradescantia paludosa* contain about ten times the DNA found in corn nuclei of the same class. The amount of DNA in *T. paludosa* leaf nuclei was compared with that found in two other closely related Tradescantia species (table 3). Both species have a haploid chromosome number of 12, twice that of *T. paludosa*, and thus it is not surprising to find the diploid nuclei contain about twice the DNA. Interspecific variation in amounts of DNA has been reported for animals and is not unexpected in view of the deletions, duplications, polysomaty, etc., considered to accompany evolution. On the same basis one would also expect the amount of DNA per nucleus might differ to some extent in various strains of the same species. To test this possibility similar tissues from two corn strains, differing in amount of heterochromatin, were mounted together and measured. Strain *A* (table 3) contained several *B* chromosomes and knobs, and the interphase nuclei showed the chromocenters associated with them.[13] Strain *B* had no *B* chromosomes and contained only a small amount of

TABLE 3

AVERAGE AMOUNTS OF DNA (FEULGEN) PER NUCLEUS IN TISSUES OF TWO STRAINS OF CORN AND THREE SPECIES OF TRADESCANTIA

	LEAF			ROOT		
	DNA IN ARBITRARY UNITS	STANDARD ERROR	NO. MEASURED	DNA IN ARBITRARY UNITS	STANDARD ERROR	NO. MEASURED
Corn strain A	6.4	0.12	15	6.6	0.08	15
Corn strain B	7.2	0.10	15	7.4	0.12	15
T. paludosa	8.5	0.08	25			
T. "virginiana"	16.8	0.20	25			
T. canaliculata	16.1	0.18	25			

heterochromatin on chromosome 6. Class 4*C* nuclei, from root and leaf, showed a difference in DNA between strains of about 10%.

Discussion.—The data presented indicate that DNA follows quantitative restrictions of the same general type reported for animal tissues. Three points may be stressed: (1) The amount per nucleus shows a marked step-like occurrence. (2) There is a duplication with mitosis and a reduction with meiosis. (3) Since species and strains have characteristic amounts of DNA it is apparent that the quantities involved are directly associated with the genotype. At least for the present these factors seem best interpreted by considering DNA as a component of the gene.

A considerable amount of recent cytological evidence has accumulated that points to the occurrence of "supernumerary chromonemal reproductions" as they have been called by Lorz[14] in numerous plant tissues. In several instances chromosomes have been described as 2, 4 or 8 stranded (polytene).[15,16] Endomitotic cycles, such as those described in the tapetum of Spinacia[17] or tomato,[18] are known to cause doubling of the chromo-

some number, and where differentiated resting nuclei have been stimulated to divide by auxins[19] or other treatment, polyploid nuclei with 2, 4, 8, etc., times the diploid chromosome number have been found. As pointed out by Schrader and Leuchtenberger it seems likely that the occurrence of varying amounts of DNA is associated with such factors.

The nuclei measured in the course of the present work naturally represent an extremely small sample. Nevertheless it is interesting that so few intermediate values have been found in non-dividing tissues. This would seem to indicate that the "endomitotic" processes, during which DNA doubling occurs, are comparatively rapid, and that unsynchronized chromonemal reproductions of the type seen in Rhoeo[19] are rare in the tissues studied. They may be more common in the older nuclei, which are often too irregular to measure.

The conclusion seems unavoidable, from both cytological and photometric evidence, that many, and in some tissues most, cells typically contain multiple chromonemal sets. The role played by these cells in the economy of the organism can at present only be conjectured. By analogy with the situation in autopolyploid plants one might expect the physiological balance to be altered. It has often been suggested that endomitotic gene doubling is associated with differentiation.[20, 21] However, in Tradescantia stamen hairs, as well as in some mammalian tissues, the higher classes do not appear until differentiation is completed.

Summary.—Photometric determinations on individual Feulgen-stained corn and Tradescantia nuclei support the view that DNA occurs in well-marked units characteristic of the strain or species. Nuclei with 2, 4, 8, 16 or 32 times the haploid (microgamete) value occur. Preceding mitosis DNA increases in interphase to twice the dipoloid amount. In meiosis the DNA is reduced, so that the microgamete contains half the diploid value.

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*ALLELISM OF SECOND CHROMOSOME LETHALS IN D. MELANOGASTER**

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Our knowledge of the genetic composition of populations, other than that of human blood group genes, is based primarily on lethal chromosomes from populations of Drosophila. Paradoxically, because of the advanced genetic techniques in Drosophila, our information for species of this genus consists of *chromosomal* frequencies although the dynamics of population genetics depends upon *gene* frequencies. It would be possible to analyze Drosophila populations for specific gene loci but it has proved more profitable to evaluate the easily collected lethal chromosome data by estimating the number of loci on a given chromosome at which lethal alleles may exist. This estimation, which can be made by determining the frequency of allelism between lethals of independent origin, has been made by Wright[1, 2] for the third chromosome of *D. pseudoobscura* (285–289 loci) and by Ives[3] for the second chromosome of *D. melanogaster* (495 loci). In connection with experimental populations which are exposed to continuous gamma irradiation, it has been necessary to determine the number of loci which are capable of mutating to lethality under the influence of these radiations.

Flies of the Oregon-R strain of *D. melanogaster* carrying lethal-free second chromosomes were placed in a population cage and were allowed to oviposit on food in small plastic cups throughout the day (8 hrs.) or overnight (16 hrs.). (See Wallace[4] for a detailed description of the cages and the cups.) At the end of each egg-collecting period, a fresh cup was exposed to the parental flies, and the old cup, with its eggs, was placed in a cage which encircled a 500-mg. radium bomb. To keep the developing flies of each cup separate from the rest, a thin-walled plastic tube was inserted into the food of each cup and was plugged at its free end with cotton.